vestigators who have accepted *F. monticola* as a distinct species include Hesse (1909), Rehder (1910), Bailey (1949), Harms (1930), Anderson and Sax (1935) and Ernst (1963). However, Anderson and Sax (1935) and Rehder (1910) pointed out that *F. monticola* might better be treated as a variety of *F. major* rather than as a species distinct from it. Ernst (1963) noted that the two are sympatric and are nearly indistinguishable, and that the relationship between them is in need of study. It is perhaps of significance that Ashe (1897), in describing *F. monticola*, considered it to be the only species of *Fothergilla* in the southern Appalachians. Indeed he states "the only published name that could possibly apply to this species [*F. monticola*] is *F. major* Lodd." It was Ashe's opinion, however, that *F. major* Lodd. was merely a robust specimen of the coastal plain species.

The status of *Fothergilla parvifolia* as a taxon distinct from *F. gardenii* is also open to question. The supposed coastal plain taxa reportedly differ in the shape and dentition of the leaves and in the length of the capsules.

Authors who have accepted *Fothergilla parvifolia* as a distinct species include Small (1903, 1913, 1933), Britton (1905), and Harms (1930). More recent authors, including Ernst (1963) and Radford *et al.* (1964) have treated *F. parvifolia* as a synonym of *F. gardenii*.

The present paper is an attempt to evaluate, both morphologically and cytologically, the taxonomy of the genus *Fothergilla*.

PHENOLOGY

The flowering period of the populations of *Fothergilla* in the coastal plain begins in late March in northern Florida and southern Alabama and continues until mid-May in North Carolina. The peak of flowering in North Carolina is during the second and third weeks of April. *F. alnifolia* (= *F. gardenii*) δ *serotina*, originally described by Sims (1810) and taken up by DeCandolle (1830) and Harms (1930) reportedly blooms in August. I have found no evidence, either from herbarium specimens or from field observations, of a *Fothergilla* blooming in August. *F. alnifolia* δ *serotina* was based on a cultivated plant, and its blooming in August was probably an abnormal occurrence.

The flowering period of the montane Fothergillas is affected by altitude as well as latitude but generally extends from late March until mid-May in various parts of their range.

The appearance of the flowers in relation to that of the leaves has been used by several authors (Small, 1903, 1913, 1933; Britton, 1905) as a key character for distinguishing the species of *Fothergilla*. It has been reported that the flowers of the coastal plants appear before the leaves, while the flowers of *F. major* appear as the leaves are unfolding. Observation of the plants in the field, as well as examination of herbarium specimens, indicates that this is generally true. Although exceptions have been noted, the distinction remains a fairly usable diagnostic character.

Van Dersal (U.S.D.A. Miscell. Publ. #303, pp. 128, 129. 1938) found that the seeds do not germinate until the second year, evidently requiring a period of low temperatures to break the dormancy of the embryo.

Flowers are initiated during the summer growing season and complete inflorescences are formed before the leaf drop in the fall. Meiosis, however, does not take place until the following spring.

MORPHOLOGY

Habit. Plants of the genus *Fothergilla*, generally low shrubs with erect or strongly ascending aërial stems, spread profusely by means of woody underground stems, frequently forming dense clumps. The aërial stems are typically unbranched for one-half to one-third their height, and in the case of the coastal plain populations may be completely unbranched. The coastal plain plants are seldom more than one meter tall, although exceptional specimens up to 2.6 meters in height have been seen; flowering specimens of the montane plants are generally between one and three meters in height, but in extreme cases may be nearly 6.5 meters tall.

Hesse (1909), Rehder (1910), and Bailey (1949) have used supposed differences in habit to distinguish *F. major* from *F. monticola*. The glaucous *F. major* is reportedly an erect, pyramidal shrub, while the nonglaucous *F. monticola* is less tall and more spreading. Examination of several populations of *Fothergilla*, consisting of both glaucous and nonglaucous plants, in the mountains of western North Carolina has given no indication of such a difference in habit. Most plants of both types are rather low, spreading shrubs. Occasionally, especially when growing in moister situations, the plants of both types become taller and more erect. The tallest and most nearly erect plant examined was nonglaucous.

On the other hand, examination of *Fothergilla* plants cultivated at the Arnold Arboretum of Harvard University has shown that several of the shrubs in the collection are indeed erect with a more or less pyramidal shape, totally different from any of the numerous plants which were studied in the field. Other plants at the Arboretum, more typical of the wild type, are low and spreading. While all of the erect plants are glaucous, the spreading plants are of both types. The significance of this difference in habit is unknown, but since it is not consistently correlated with the presence or absence of a waxy bloom on the undersides of the leaves, it should be ruled out as a character substantiating the existence of two taxa of *Fothergilla* in the mountains of the southeastern United States.

Vestiture. The undersides of the leaves of both the montane and coastal plain forms of *Fothergilla* are occasionally covered with a fine, waxy bloom. As mentioned earlier, the presence or absence of this bloom has been used as the primary morphological character for distinguishing *F. major* from *F. monticola*.

Since the waxy bloom generally disappears when specimens are heat dried, and since most collectors regrettably have failed to mention whether

or not the plants were glaucous, herbarium specimens are useless for the study of this character. Therefore field studies were necessary. Populations were studied in the following localities:

PIEDMONT

1. Near Hillsborough, Orange County, North Carolina.
2. Hanging Rock State Park, Stokes County, North Carolina.

MOUNTAINS

3. Gorge of the Thompson River, Transylvania County, North Carolina.
4. Gorge of the Horsepasture River, Transylvania County, North Carolina.

The Piedmont populations are composed entirely of nonglaucous individuals; the mountain populations are composed of approximately equal numbers of glaucous and nonglaucous individuals. There appears to be little variation in the amount of bloom among those plants which are glaucous at all; the bloom when present is very striking and in all probability is genetically controlled. Aside from the presence or absence of a waxy bloom the plants are indistinguishable as far as leaf, capsule, and habital characters are concerned. In view of this fact and since glaucous and nonglaucous individuals grow side by side in the same population, this single character seems to offer insufficient grounds for the recognition of two taxa of any rank.

A single population of *Fothergilla* in the coastal plain of North Carolina (Scotland County) was found to consist of glaucous and nonglaucous individuals. As in the case of the montane populations both types grow side by side and are identical in other respects.

The aërial organs of *Fothergilla*, both floral and vegetative, with the exception of the styles and stamens, are clothed to varying degrees with a soft, downy pubescence. The individual trichomes are stellate in form, composed of six to ten unicellular segments radiating from a single modified epidermal cell. The color of the trichomes varies from dark brown on the stipules and floral bracts to a pale yellow on the remaining parts. Interspersed among the stellate trichomes on the apex of the ovary and persisting on the mature fruit are stiff, yellow, simple trichomes which are apparently the only simple ones to be found on the plant.

In general the coastal plain plants are pubescent to a greater degree than are the montane plants; however, in both groups the amount of pubescence varies among the respective organs, as well as on the same organ of different plants. The trichomes are generally dense and overlapping on the petioles, stipules, calyx, floral bracts, and peduncles. The aërial stems of the montane plants are generally pubescent on the distal portions, especially at the bases of the spikes and the leaves where the pubescence may be considerable, and on the present year's growth, but become completely glabrous in the proximal portions; those of the coastal plain plants are frequently pubescent, at least sparingly so, to the base.

The leaves are pubescent on both surfaces, but generally more densely so on the abaxial surface; the trichomes are scattered to varying degrees over the lamina but are often concentrated on the principal veins or in their axils. The lamina is frequently glabrous in the montane plants but is always pubescent to some degree in the coastal plain plants examined.

Rehder (1910) reported that the leaves of *F. major* varied from scattered to rather densely pubescent beneath, while those of *F. monticola* were pubescent chiefly on the veins, the lamina often being nearly glabrous. Ernst (1963) also noted that *F. monticola* was pubescent to a lesser degree than *F. major*. Bailey (1949) was vague on the matter, having described the leaves of *F. major* as pubescent below, at least on the veins, as opposed to scattered pubescent below in *F. monticola*.

Examination of herbarium specimens as well as observations of the plants in the field has indicated that the degree of pubescence of the leaves on an individual plant of both the glaucous and nonglaucous types is quite variable. For example, the pubescence on the undersides of the twenty-five mature leaves taken at random from plants of both the glaucous and nonglaucous types in each of two populations in Transylvania County, North Carolina, demonstrated that the range of variation in the degree of pubescence is the same for both types: in each of the plants studied the variation ranges from leaves in which the lamina is glabrous to leaves in which the lamina is covered with a nearly continuous indumentum.

In order to quantify these impressions herbarium specimens prepared from two populations of *Fothergilla* (one from Burke County and one from Transylvania County, North Carolina) were studied intensively, and the number of trichomes present on four square millimeters of laminal surface at comparable positions on the undersides of the leaves of both the glaucous and nonglaucous types was counted. The results are summarized in TABLE 1.

TABLE 1. **Variation in the Number of Trichomes on the Leaves in Two Populations of the Montane Fothergilla**

LOCALITY	COLLECTOR AND NUMBER	FORM	NUMBER OF LEAVES	RANGE OF VARIATION IN # OF HAIRS	MEAN # OF HAIRS
Burke Co.	*Wilbur 7040*	glaucous	40	0–40	5.09
Burke Co.	*Wilbur 7038*	nonglaucous	40	0–30	5.98
Transylvania Co.	*Weaver 300*	glaucous	20	7–35	16.65
Transylvania Co.	*Weaver 301*	nonglaucous	20	4–29	13.55

From the data in TABLE 1 the following conclusions may be drawn as far as the populations studied are concerned: (1) the variation in degree of pubescence of each form is great within one population as well as between different populations; (2) the variation in the degree of pubescence of each form is approximately equal in each population.

Even though the samples were small the results indicate that there is no consistent difference in the degree of pubescence between glaucous and nonglaucous individuals.

Leaves. The leaves of *Fothergilla* are simple, alternate, deciduous and somewhat coriaceous in the coastal plain populations, while they are thinner and membranaceous in the montane populations. Variation in shape and type of dentition is great; it is not at all unusual to find on a single plant leaves with (1) shape ranging from elliptic through ovate and obovate to suborbicular; (2) bases cordate, truncate, and rounded; (3) apices acute, obtuse, and emarginate; and (4) margins varying from coarsely serrate-dentate to entire. Extent of the dentition, however, is more nearly constant than the type of dentition; in general among the coastal plain populations the dentition when present is restricted to the upper half of the leaf, while among the montane populations it almost invariably extends below the middle of the leaf.

Leaf size has traditionally been used to distinguish the montane and coastal plain forms of *Fothergilla*, and it remains a usable diagnostic character. The leaves of the coastal plain plants are typically and usually conspicuously smaller than those of the montane plants. Although there is a considerable overlap in absolute leaf lengths and width between the two forms, the largest leaf on any given specimen examined from the coastal plain never exceeded 5.2 cm. in width, while the largest leaf on a specimen from the mountains was never less than 5.1 cm. wide.

Fothergilla parvifolia, described by Kearney (in Small, 1903), has usually been distinguished from *F. gardenii* by the shape and dentition of the leaves. Britton (1905) and Small (1933) agreed that the leaves are different: *F. parvifolia* with leaves broadly ovate, oval, or suborbicular, toothed mainly from below the middle, and cordate at the base; and *F. gardenii* with leaves oblong, oblong-ovate, or ovate-orbicular, toothed above the middle, and narrowed at the base, according to Britton, and elliptic, elliptic-ovate, or elliptic-orbicular, toothed only near the apex, and cuneate or rounded at the base, according to Small. Earlier, however, Small (1903, 1913) had reported that the leaf margins of *F. parvifolia* were coarsely crenate above the middle, while those of *F. gardenii* were undulate or coarsely toothed near the apex.

As may be inferred from these conflicting descriptions the distinctions, at least as regards leaf shape and dentition, between *F. parvifolia* and *F. gardenii* are hazy at best. In view of the variation among the leaves of an individual plant as described above, it would seem that the delimitation of taxa of *Fothergilla* on the basis of leaf shape and dentition is unwarranted.

Flowers. The perianth of *Fothergilla* is greatly reduced, consisting of a gamosepalous calyx, the 5–7 lobes of which are reduced to minute, irregularly shaped teeth. Petals are lacking. The base of the androecium is adnate to the calyx, forming a shallowly campanulate hypanthium. The stamens vary in number from 12–32, and are arranged in a single series on the rim of the hypanthium. The coastal plain populations tend to have fewer stamens than the montane populations; in the material studied the number ranged from 12 to 24 in the coastal plain plants and from 18 to 32 in the montane plants. The filaments, easily the most conspicuous parts of the flower, vary greatly in length with no apparent pattern in a single flower. The longer ones are conspicuously thickened distally while the shorter ones tend to be nearly filiform. The pistil is made up of two carpels fused below but divergent near the apex of the ovary into separate filiform styles.

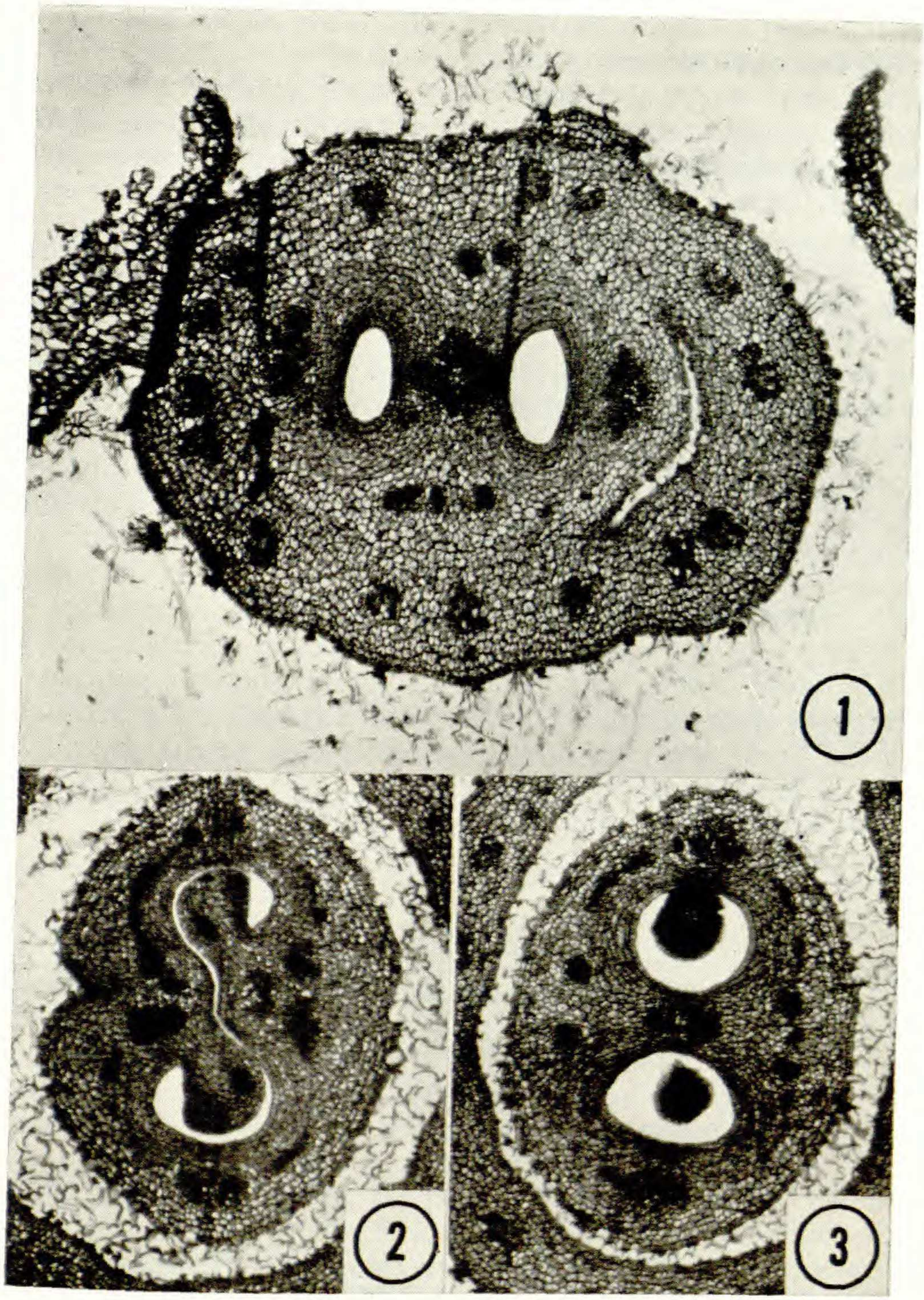
Most previous authors have considered the ovary of *Fothergilla* to be weakly perigynous; Ernst (1963) described the ovary as being "slightly recessed in the receptacle" but considered the fruit to be "partly inferior." Macroscopic examination of the ovary indicates that it is partially fused to the receptacle and is therefore semi-inferior.

In order to determine the histological relationship between the ovary and the hypanthium, flowers of *Fothergilla major* collected in Transylvania County, North Carolina, and preserved in 70% ethyl alcohol were dehydrated using the tertiary butyl alcohol series suggested by Johansen (1940), and infiltrated with paraffin. The material was sectioned on a rotary microtome at 12 microns and stained in 1% safranin in 95% ethyl alcohol and 1% fast green in 95% ethyl alcohol. The investigations have shown that the hypanthium is actually adnate to the ovary to a point slightly above the base of the ovary, i.e., at least one-third the total length of the latter (FIG. 1). Therefore the ovary is, indeed, somewhat semi-inferior.

Serial sections of the pistil have given further insight into the morphology of that organ. Macroscopically the pistil in cross section appears to be 2-locular; to my knowledge all previous authors have described the pistil accordingly.

Actually, as shown in FIGURES 2 and 3, the closure of the individual carpels is not complete from a point immediately below the attachment point of the ovules to the apex of the ovary. As a result the ovary appears to be bilocular below the attachment point of the ovules but unilocular above it. In actuality, then, the ovary is characterized by having a single deeply lobed locule. Horne (1914) reported that a similar situation, but in reverse, i.e. unilocular below and bilocular above, was found in *Rhodoleia*, a member of the subfamily Bucklandioideae of the Hamamelidaceae native of eastern Asia; he also stated, however, that the Hamamelidoideae, of which *Fothergilla* is a member, possessed septa, rendering them bilocular.

Fruits and seeds. The fruit of *Fothergilla*, a grayish or brownish loculicidal capsule, is rendered partly inferior by the fusion of the per-



FIGURES 1–3, Cross section of the flower of *Fothergilla major*, × 60. FIG. 1, Fusion of the ovary to the hypanthium. FIG. 2, Ovary at attachment point of the ovules. FIG. 3, Ovary below attachment point of the ovules.

sistent hypanthium to the ripened ovary. Each of the carpels dehisces along a median dorsal suture, and, as a result, the capsule is 4-beaked at maturity. The capsules of the montane and coastal plain forms are similar in shape, but those of the montane populations are decidedly larger in size. Although there is a considerable overlap in total capsule length in the material at hand, the fruiting hypanthium of the coastal plain form

varies from 3 to 4.5 mm. in length while that of the montane form varies in length from 4 to 9.2 mm.

Small (1903, 1913, 1933) and Britton (1905) reported that the capsules of *Fothergilla parvifolia* varied from 6 to 8 mm. in length, while those of *F. gardenii* varied from 8 to 10 mm. Examination of specimens from Jesup, Georgia, the type locality of *F. parvifolia*, including a specimen identified as *F. parvifolia* by Kearney (*Kearney s.n.*, 1893 [NY]) has shown that the capsules of these plants actually vary from 7 to 10 mm. in length. In addition numerous capsules of typical *F. gardenii* measuring less than 8 mm. have been seen.

Rehder (1947) and Bailey (1949) reported that the capsules of *Fothergilla major* were light brown inside with red markings on the inner sutures, while those of *F. monticola* were darker inside without the red markings. Examination, in the field, of the capsules of the glaucous and nonglaucous forms of the montane *Fothergilla* shows that the color of the inside of the capsules often varies from light to dark brown on the same plants. The red markings reported by Rehder and Bailey are indistinct at best and are not constant even among the capsules of a single inflorescence.

The seeds of *Fothergilla*, two per capsule at maturity, are ellipsoid or narrowly ovoid with a very hard, shiny, reddish-brown seed coat. A whitish area, decurrent on opposite sides of the seed and including the sub-apical hilum, is present at the micropylar end. In the material examined, the seeds of the montane populations vary in length from 6.2 to 7.8 mm., while those of the coastal plain populations vary from 4.8 to 6.3 mm. in length.

CYTOLOGY

The first account known to me of the chromosome number of any of the species of *Fothergilla* is that of Anderson and Sax (1935) in their survey of the chromosome numbers in the Hamamelidaceae. They reported the haploid number to be $n = 36$ for *F. major* and $n = 24$ for *F. monticola*. The counts were made from aceto-carmine smears of pollen mother cells from plants growing at the Arnold Arboretum of Harvard University. Anderson and Sax pointed out, however, that the "species" are so similar that it is doubtful whether *F. monticola* deserves more than varietal rank. It was their opinion, from the cytological evidence, that "*F. monticola* is merely a tetraploid variety which arose spontaneously from the hexaploid species, *F. major*."

Thomas (in Ernst, 1963) also reported the chromosome numbers of *Fothergilla*, the counts again having been made from plants growing at the Arnold Arboretum. His results were as follows:

SPECIES	ARNOLD ARBORETUM ACCESSION NUMBER	HAPLOID NUMBER
F. monticola	AA # 4163–A	$n = 24$
F. major	AA # 694–34	$n = 36$
F. gardenii	AA # 684–50	$n = 36$

In the course of this study the chromosomes of *Fothergilla* were again recounted. Inflorescence buds were originally collected during April, 1966. In addition buds of *F. gardenii* were obtained from Mrs. Anne B. McCrary, of Wilmington, N.C. All buds were fixed in modified Carnoy's Solution (3 parts absolute ethyl alcohol: 1 part glacial acetic acid) and stored under refrigeration in 70% ethyl alcohol.

FIGURES 4 and 5, Meiotic chromosomes of *Fothergilla*, × 1500. FIG. 4, *F. gardenii*, $n = 24$, Telophase I, *Weaver 350*. FIG. 5. *F. major*, $n = 36$, Metaphase II, *Weaver 1294*.

Since the waxy bloom is not yet developed on newly expanding leaves, the montane forms are indistinguishable from one another while in bud. Therefore it was necessary to mark the plants from which the buds were collected and to return later in the season to determine whether the plants were glaucous or nonglaucous. Unfortunately all buds collected in 1966 were from nonglaucous plants. Glaucous plants were located in Transylvania County, N.C., and tagged during August, 1966. These plants were relocated in April, 1967, when buds were collected.

Voucher specimens were made from plants in the immediate population from which the buds were taken. Wherever possible floral specimens were made at the time the buds were collected. In addition most of the populations were revisited later in the season and vegetative or fruiting specimens were made.

My investigations have shown that, in general, inflorescence buds contain anthers undergoing sporogenesis as long as the stamens of none of the individual flowers exceed the subtending bracts. Buds at this stage are generally less than 1 cm. long.

All counts were made from aceto-carmine squashes of pollen mother cells. The results of the study are summarized in TABLE 2.

TABLE 2. **Chromosome Numbers of Fothergilla**

COASTAL PLAIN FORMS:

COLLECTOR AND NUMBER	LOCATION	HAPLOID NUMBER	NUMBER OF COUNTS
Weaver 355 (DUKE, GH, MICH)	Scotland Co., N.C.	$n = 24$	2
McCrary (No Voucher Made)	New Hanover Co., N.C.	$n = 24$	2
Weaver 350 * (DUKE, GH, MICH)	Scotland Co., N.C.	$n = 24$	4

MONTANE FORMS:

FORM	COLLECTOR AND NUMBER	LOCATION	HAPLOID NUMBER	NUMBER OF COUNTS
Nonglaucous	*Weaver 330* (DUKE, GH, US)	Orange Co., N.C.	$n = 36$	2
Nonglaucous	*Weaver 460* (DUKE)	Stokes Co., N.C.	$n = 36$	2
Nonglaucous	*Weaver 360* (DUKE, GH)	Transylvania Co., N.C.	$n = 36$	4
Glaucous	*Weaver 370* (DUKE, GH)	Transylvania Co., N.C.	$n = 36$	1

* See FIG. 4 for a photograph of the chromosomes of this plant.

TABLE 3. **Chromosome Numbers of Fothergilla Plants at the Arnold Arboretum**

ARNOLD ARBORETUM ACCESSION NUMBER	FORM	HAPLOID NUMBER	NUMBER OF COUNTS	VOUCHER
4163–A *	Nonglaucous	$n = 36$	15	*Weaver 1294* (DUKE)
4163–C	Nonglaucous	$n = 36$	2	*Weaver 1295* (DUKE)
577	Glaucous	$n = 36$	2	*Weaver 1296* (DUKE)
326–49–A	Glaucous	$n = 36$	2	*Weaver 1297* (DUKE)
694–34–A	Glaucous	$n = 36$	2	*Weaver 1298* (DUKE)
695–34–A	Nonglaucous	$n = 36$	2	*Weaver 1299* (DUKE)
14610–A	Glaucous	$n = 36$	2	*Weaver 1300* (DUKE)
1265–62–B	Nonglaucous	$n = 36$	2	*Weaver 1301* (DUKE)

* See FIG. 5 for photograph of the chromosomes of this plant.

Since Thomas recorded the accession numbers of the plants from which his counts were made, a direct check on his work is possible. Preserved inflorescence buds from *Fothergilla* plants at the Arnold Arboretum were obtained by Dr. Carroll E. Wood, Jr., who most generously placed them at my disposal. Chromosome counts were made from aceto-carmine smears of pollen mother cells as before. The plants from which the counts were made were examined at the Arboretum and voucher specimens were made. The results of this investigation are summarized in TABLE 3.

My counts for AA 4163–A are in striking disagreement with those of Thomas. The possibility that the plant might be a mixed clump of coastal plain and montane plants has been ruled out by a personal examination of the plant at the Arnold Arboretum. Considering that pairing of the chromosomes at Metaphase I appeared normal in all the cells examined, the possibility of an aberrant meiotic division of the magnitude necessary to produce a cell containing 24 chromosomes instead of the normal 36 is very slight. There seems to be no alternative than to suggest that the previous counts were in error.

The culture AA 684–50 is no longer present among the collections at the Arnold Arboretum. However, the accession data of this plant shows that the plant was originally collected on Crowder's Mountain, Gaston County, North Carolina. This locality is in the upper Piedmont and hence is considerably outside of the range of the coastal plain species of *Fother-*

gilla. Since typical *F. major* has been collected on Crowder's Mountain (*Beadle s.n.*, 1938 [NCU]; *Biltmore Herb. 708g* [NY]), it seems very likely that AA 684–50 was misidentified. The previously reported haploid number of $n = 36$ for the coastal plain species of *Fothergilla* should be disregarded as a valid count; the specimen from which the count was derived is, in all probability, the montane *F. major*.

As Anderson and Sax neither prepared voucher specimens nor reported the accession numbers of the plants from which their counts were made (C. E. Wood, Jr., *in litt.*), a direct check on their work is impossible. However, the present study would suggest either that the count by Anderson and Sax for "*F. monticola*" was incorrect, or more probably that the plant from which the count was made was in fact a specimen of the coastal plain plant rather than *F. monticola* as reported.

On the basis of the cytological and morphological investigations carried out in this study, there seems to be no basis whatever for the recognition of separate taxa of any rank within either the coastal plain or the Appalachian Highlands populations of *Fothergilla*.

SYSTEMATIC TREATMENT

Fothergilla Murray in Linn. Syst. Veg. ed. 13. 418. 1774.

Yongsonia W. Young, Cat. Arb. Arbust. 54. 1783, *nomen illegit.* Art. 32.
Foterghilla Dumort. Anal. Fam. 35. 1829.
Fothergillia Spreng. in Linn. Gen. Pl. ed. 9. **1:** 445. 1830.

Stellate-pubescent, often clump-forming shrubs, proliferating by means of woody underground stems. Roots fibrous, adventitious from the bases of the aërial stems or from nodes on the underground stems. Aërial stems erect or strongly ascending, unbranched in the lower portions, sparsely or profusely branched in the upper portions, occasionally entirely unbranched; branches proliferating or strongly ascending. Bark smooth, reddish-brown with conspicuous whitish lenticels in younger growth, uniformly light gray in older growth. Vegetative buds naked. Leaves alternate, deciduous, simple, petiolate, membranaceous or somewhat coriaceous, pale green or glaucous beneath, typically elliptical or obovate, more rarely oblong, ovate, or suborbicular; margins coarsely crenate or serrate-dentate, occasionally undulate or even entire; apices acute or obtuse, rarely retuse; bases often unequal, typically obtuse or cordate, occasionally truncate; veins pinnate, alternate or sub-opposite, the 4 to 6 pairs often excurrent into short mucros. Stipules chaffy, narrowly lanceolate to ovate, shortly deciduous. Inflorescence a dense, erect ament-like spike, sessile or short-pedunculate, terminal but often borne on very short lateral shoots and seeming axillary, appearing with the leaves or before them. Inflorescence buds enclosed by an ovate or lanceolate, frequently tridentate scale, which is persistent on the mature inflorescence and generally subtends the lowermost flower. Flowers mostly perfect, but the lower ones frequently female-sterile due to the presence of an abortive pistil, subtended by an ovate to suborbicular,

densely brownish-tomentose, soon deciduous bract. Petals lacking. Calyx gamosepalous, adnate to the androecium to form a shallowly campanulate hypanthium; lobes 5 to 7, reduced to minute, irregularly shaped teeth. Inner rim of the hypanthium encircled by a series of very minute, fleshy teeth. Stamens indefinite in number, varying from 12 to 32, apparently inserted in a single series on the rim of the hypanthium; filaments white, conspicuous, unequal in length, the longer ones conspicuously expanded distally, the shortest ones nearly filiform, all greatly exserted; anthers yellow, often becoming purple with age, cuboidal to pyramidal in shape, innate with 4 pollen sacs but becoming 2-locular at anthesis, dehiscent by 2 longitudinal flaps along an I-shaped suture; connective inserted. Pistil 2-carpellate, the carpels connate below but divergent near the apex of the ovary into 2 separate styles; ovary semi-inferior, adnate to the hypanthium for about one-third of its total length, shallowly bilobed, unilocular, the locule deeply bilobed and appearing 2-locular below the attachment of the ovules; styles exceeded by the longest stamens, persistent, subulate-filiform, slightly expanded distally, the stigmatic surfaces linear, introrsely decurrent. Ovules anatropous, 2-integumented, the micropyle facing upwards, at anthesis 2 per ovary on parietal placentae. Fruit a grayish to brownish loculicidal capsule 4-beaked at maturity with the lustrous, bony endocarp distinct from but not separating from the exocarp, semi-inferior, the ripened ovary adnate more or less to the middle with the persistent hypanthium. Seeds 2 at maturity, ellipsoid or slightly ovoid; seed coat very hard, smooth, shiny, reddish-brown; hilum subapical, surrounded by a whitish area; endosperm very hard, white. TYPE SPECIES: *F. gardenii* Murray.

KEY TO THE SPECIES OF FOTHERGILLA

1. Earliest flowers appearing with the leaves; leaves generally toothed only in upper half, rarely asymmetric at base, the largest ones never more than 5.2 cm. wide; stamens generally 12–24; hypanthium at anthesis 1.5–2.6 mm. wide and 0.9–1.5 mm. deep; fruiting hypanthium 3–4.5 mm. long; seeds 4.8–6.3 mm. long. Atlantic and Gulf Coastal Plains from North Carolina to Florida and Alabama. ..... 1. *F. gardenii.*

1. Earliest flowers appearing with the leaves; leaves generally toothed from below the middle, conspicuously asymmetric at base, the largest ones not less than 5.2 cm. wide; stamens generally 22–32 in number; hypanthium at anthesis 2.4–3.9 mm. long and 1.5–3 mm. deep; fruiting hypanthium 4–9.2 mm. long; seeds 6.2–7.8 mm. long. Mountains and Piedmont from North Carolina to Alabama. ..... 2. *F. major.*

1. **Fothergilla gardenii** Murray in Linn. Syst. Veg. ed. 13. 418. 1774 [as *F. Gardeni*].

Hamamelis virginiana carolina L. Mant. Pl. Alt. 333. 1771.
Fothergilla alnifolia L.f. Suppl. Pl. 52. 1781, *nomen illegit.* Art. 63.
F. alnifolia α *obtusa* Ait. Hort. Kew. 2: 241. 1789.
F. alnifolia β *acuta* Ait. *Ibid.*

F. alnifolia δ *serotina* Sims, Bot. Mag. **33**: *t. 1341*. 1810.
F. carolina (L.) Britton, Mem. Torrey Bot. Club **5**: 180. 1894.
F. parvifolia Kearney in Small, Fl. Se. U.S. 509. 1903.

Plants stellate-pubescent, the undersides of the leaves occasionally glaucous. Aërial stems solitary or in clumps, simple or sparingly to ± profusely branched in upper portions, in flowering specimens 0.3–2 cm. in diam. and 2.5–10(26) dm. tall, densely brown pubescent in distal portions, glabrous or occasionally sparingly pubescent in proximal portions. Underground stems unbranched or sparsely branched, 0.5–2 cm. in diam. Leaf blades coriaceous in texture, 0.9–6.3 (9.8) cm. long and 0.7–4.1(5.2) cm. wide, sparsely to densely yellow or rusty pubescent on both surfaces, but generally more so below, never glabrous, variable in shape, most often elliptical or oblong but not infrequently ovate, obovate, or suborbicular; margins frequently entire or undulate, but equally frequently coarsely crenate or serrate-dentate, the dentition when present generally restricted to upper half of blade, the teeth often ending in short mucros; apices generally acute or obtuse, occasionally retuse or emarginate; bases obtuse or truncate, rarely cordate or asymmetrical. Petioles densely yellow-pubescent, 1–11(14) mm. long. Stipules lanceolate or lance-ovate, 1.5–4(6.1) mm. long, moderately to densely brown-pubescent. Spikes generally appearing before the leaves begin to unfold, (1.1)2.2–4.4(5.2) cm. long and 1.6–3 cm. wide, elongating as flowering progresses, sessile or short-pedunculate, the peduncles then up to 6.2 mm. long and densely yellow-pubescent. Floral bracts ovate or suborbicular, densely brown-pubescent, the lowermost 4.1–7.9 mm. long and 2–6 mm. wide, the others 2.2–5.1 mm. long and 1.7–3.5 mm. wide. Calyx lobes 5–7, minute and inconspicuous, at anthesis less than 1 mm. long. Hypanthium at anthesis 1.5–2.6 mm. wide and 0.9–1.5 mm. deep, densely yellow-pubescent. Stamens 12–24; filaments (2.8)4.5–12(15.8) mm. long, 0.2–0.8 mm. wide; anthers 0.5–1 mm. long, 0.4–0.9 mm. wide. Styles and stigmas together 4.5–10.5 mm. long. Ovary at anthesis 1–2 mm. long, densely yellow-pubescent. Capsules 6.5–10.5(13) mm. long, the persistent hypanthium 3–4.5 mm. long and 4–7(8.8) mm. wide; beaks 3.5–6(8.7) mm. long. Seeds 4.8–6.3 mm. long and 2.3–3.2 mm. wide. $2n = 48$.

Margins of swamps in the Atlantic and Gulf Coastal Plains from Central North Carolina to eastern Alabama (FIG. 6).

REPRESENTATIVE COLLECTIONS. **North Carolina.** Beaufort Co.: *Sawyer 2475* (NCU); Bladen Co.: 1.5 mi. nw. of Bladenboro, *Ahles 23593* (NCU); Brunswick Co.: 5 mi. n. of Orton, *Bell 11546* (NCU); Carteret Co.: 14 mi. w. of Morehead City, *Wilbur 6924* (DUKE); Craven Co.: Bridgeton, *Radford 31924* (GH, NCU); Columbus Co.: 6 mi. nw. of Pireway, *Bell 11417* (NCU); Cumberland Co.: Fayetteville, *Biltmore Herbarium 7609h* (US); Duplin Co.: 3.2 mi. ese. of Kenansville, *Radford 23990* (NCU); Harnett Co.: 1.5 mi. s. of Spout Springs, *Radford 8380* (NCU); Hoke Co.: 8 mi. ne. of Dundarrach, *Ahles 29627* (NCU); Lee Co.: 1 mi. s. of Juniper Spring Church, *Stewart 451* (NCU); Montgomery Co.: 2.5 mi. e. of Norman, *Radford 19633* (NCU); Moore Co.:

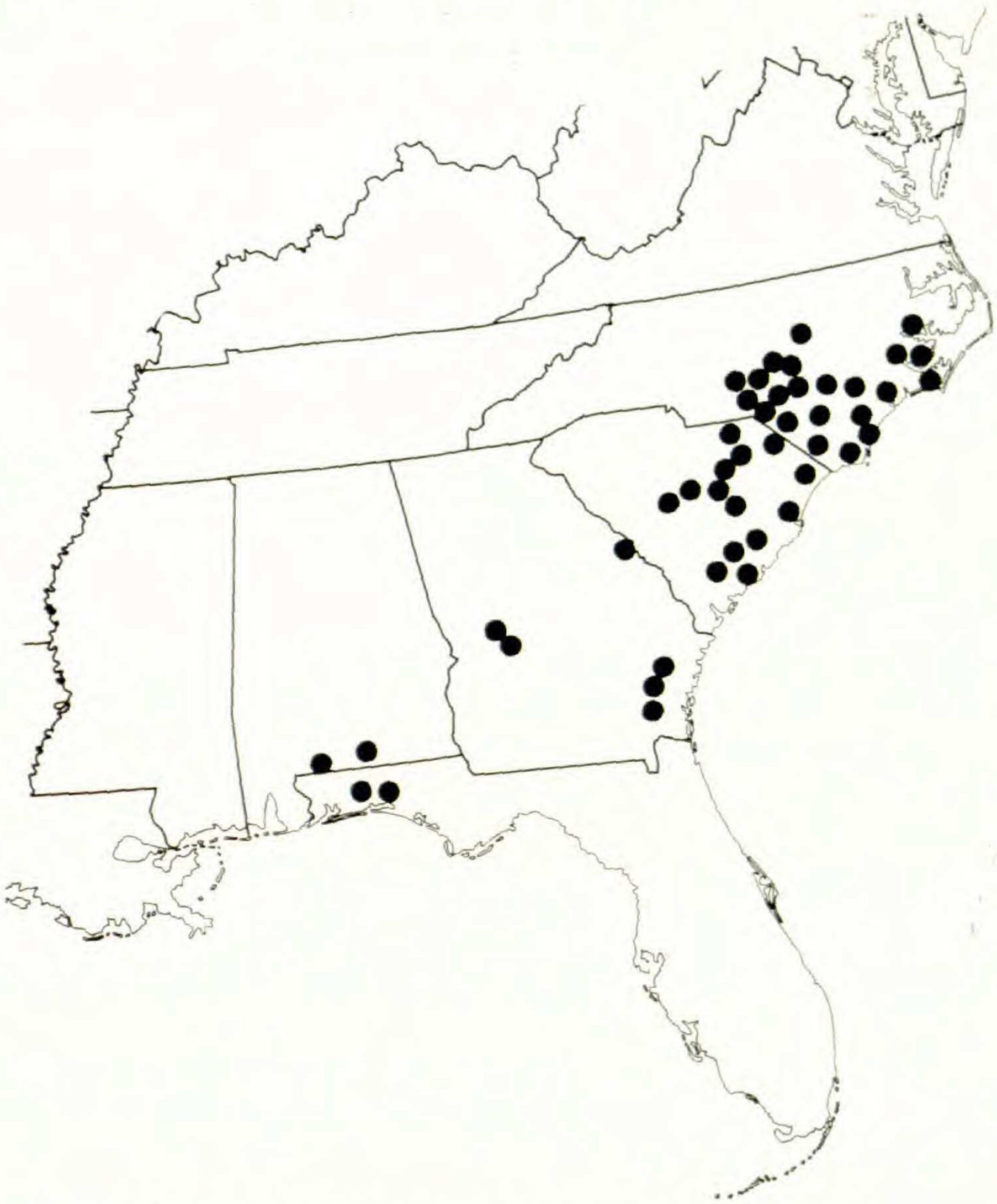


FIGURE 6, Distribution of *Fothergilla gardenii* Murr.

10 mi. s. of Aberdeen, *Coker*, 20 April 1942 (NCU); Onslow Co.: 5 mi. e. of Camp Cowhorn, *Boyce & Moreland 647* (GH, NY); Pamlico Co.: 5.2 mi. n. of Grantsboro, *Radford 42285* (NCU); Pender Co.: 2.7 mi. ne. of Hampstead, *Ahles 23440* (NCU); Richmond Co.: 3.1 mi. e. of Ellerbe, *Gupton 1286* (NCU); Robeson Co.: 2.5 mi. ssw. of Pembroke, *Terrell 3019* (NCU); Sampson Co.: 7.4 mi. n. of Delway, *Radford & Stewart 176* (NCU); Scotland Co.: just s. of bridge over Lumber Creek on US 15–501, *Weaver 355* (DUKE, GH, MICH); Wake Co.: Raleigh, *Hyanis 1898* (NY). **South Carolina.** Berkeley Co.: 16 mi. ne. of Charleston, *Duncan 5923* (GA, GH, MO); Charleston Co.: 1.5 mi. n. of Ravenel, *Duncan 5885* (GA, MO); Chesterfield Co.: just e. of Middendorf, *Oosting 340* (DUKE); Clarendon Co.: 1 mi. nw. of Turbeville, *Radford 21097* (NCU); Colleton Co.: *Bell 1862* (FSU, GA, NCU); Darlington Co.: Dovesville, *Smith 1374* (NCU); Dillon Co.: .5 mi. e. of Dillon, *Radford & Stewart 56* (NCU); Dorchester Co.: w. of Ridgeville, *Ahles 31966* (NCU); Georgetown Co.: 2 mi. w. of Georgetown, *Weatherby & Griscom 16548* (GH); Horry Co.: 10 mi. n. of Myrtle Beach, *Griscom 16547* (A, GH, NY); Lee Co.: .2 mi. n. of Lucknow, *Radford*

27396 (NCU); Lexington Co.: 3.5 mi. ne. of Gaston, *Radford 23378* (NCU); Richland Co.: Columbia, *Philson*, 20 April 1936 (GA); Sumter Co.: *Rehder 954* (A). **Georgia.** Brantley Co.: near Schlatterville, *Thorne & Norris 6284* (GH); Long Co.: 4 mi. w. of Glennville, *Duncan 2222* (GA); Macon Co.: 5 mi. s. of Reynolds, *Pyron & McVaugh 1521* (GA, US); Richmond Co.: near Augusta, *Sargent*, 24 April 1900 (A); Taylor Co.: 6 mi. sw. of Butler, *Duncan 5115* (GA); Wayne Co.: *Duncan 1986* (GA). **Florida.** Okaloosa Co.: on US 90 in Crestview, *Stone 2586* (DUKE, GH); Walton Co.: DeFuniak Springs, *Biltmore Herbarium 7609e* (US). **Alabama.** Covington Co.: about 2 mi. s. of Andalusia, *Harper 108* (GH, MO, US, NY); Escambia Co.: Atmore, *Blanton 206* (A).

Although *Fothergilla* must take its nomenclatural starting point with Murray's description (1774) of *F. gardenii*, Linnaeus apparently confused *Fothergilla* with *Hamamelis* and on two occasions prior to 1774 included a plant fitting the description of *Fothergilla* in his characterization of *Hamamelis virginiana*.

In his account of *Hamamelis virginica* (= *H. virginiana*) Linnaeus (Syst. Nat. ed. 12. 129. 1767) enumerated the characters of a plant sent to him by Dr. Garden of Charleston, South Carolina, which he considered to be very similar to *H. virginiana*. The plant in question, which Linnaeus described as being apetalous with 20 to 40 long, yellowish, filiform stamens, is definitely a *Fothergilla*. Linnaeus, however, did not propose a new name for the plant.

Later, Linnaeus (Mant. Pl. 2: 333. 1771) described two varieties of *Hamamelis virginiana*, of which the second, *carolina*, characterized as being apetalous with many stamens and a spicate inflorescence, is again, definitely, a *Fothergilla*. Britton (Mem. Torrey Bot. Club 5: 180. 1894), working under the American Code, took up the epithet *carolina* as the legitimate name for the plant previously known as *Fothergilla gardenii* Murr., but later (1905) evidently changed his mind and treated *F. carolina* (L.) Britton as a synonym of *F. gardenii*. Under the present International Code (Art. 60) the epithet *carolina* does not have priority except in the rank of variety and therefore should not be considered as the name for a species of *Fothergilla*.

2. **Fothergilla major** Loddiges Bot. Cab. 16: 6. *t. 1520*. 1829.
F. alnifolia γ *major* Sims, Bot. Mag. 33: *t. 1341*. 1810.
F. monticola Ashe, Bot. Gaz. 24: 374. 1897.

Plants stellate-pubescent, the undersides of the leaves frequently glaucous. Aërial stems in clumps of 3–9, sparingly branched in upper portions, never simple, in flowering specimens 0.3–3.5 cm. in diam. and 0.8–6.2 m. tall, densely brown-pubescent at base of leaves and peduncles, more sparingly so on new growth, completely glabrous in proximal portions. Underground stems unbranched or sparingly branched, 0.3–4.3 cm. in diam. Leaf blades membranaceous, 2.5–13.2(14.4) cm. long and 1.8–11.2 (13.4) cm. wide, moderately to sparsely yellow-pubescent on both surfaces, or lamina glabrous and trichomes present only on veins, variable in shape,

typically broadly elliptic or suborbicular but often ovate or obovate; margins entire or undulate to coarsely crenate or serrate-dentate, the dentition when present typically extending below the middle of the blade, rarely restricted to upper half, the teeth typically ending in short mucros; apices acute or obtuse, occasionally retuse or emarginate; bases obtuse or subcordate, conspicuously unequal. Petioles densely yellow-pubescent, 3–15(18) mm. long. Stipules lanceolate or ovate-lanceolate, 2.8–7(10.2) mm. long and 2.1–3.8 mm. wide, moderately to densely brown-pubescent. Spikes generally appearing with the leaves, rarely before them, 1–5(6.4) cm. long and 1.1–3.9 cm. wide, elongating as flowering progresses, sessile or short-pedunculate, the peduncles to 12 mm. long and densely yellow-pubescent. Floral bracts broadly ovate or suborbicular, densely brown-pubescent, the lowermost 4.1–12 mm. long and 3.5–8.8 mm. wide, the others 1.5–5.9 mm. long and 1.9–3.6 mm. wide. Calyx lobes at anthesis 0.4–1.6 mm. long. Hypanthium at anthesis 2.4–3.9 mm. wide and 1.5–3

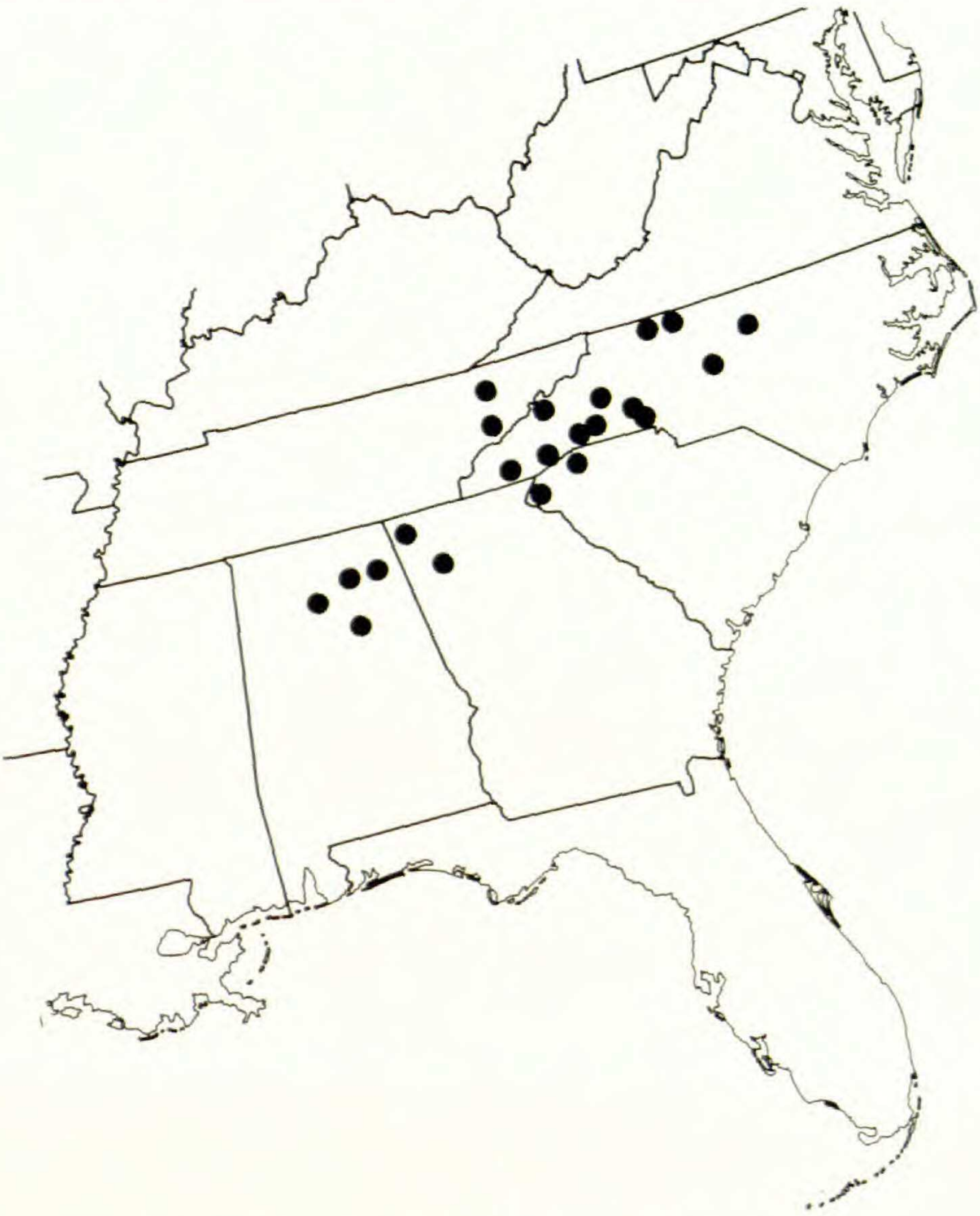


FIGURE 7, Distribution of *Fothergilla major* Lodd.

mm. deep, densely yellow-pubescent. Stamens (18)22–32; filaments 2–16 mm. long, 0.3–1.2 mm. wide. Styles and stigmas together 6.2–12 mm. long. Ovary at anthesis 1.5–2.2 mm. long, densely yellow-pubescent. Capsules 8–15.2 mm. long, the persistent hypanthium 4–9.2 mm. long, 6–8.6 mm. wide; beaks 4.9–8.3 mm. long. Seeds 6.2–7.8 mm. long, 2.7–3.5 mm. wide. $2n = 72$.

Dry rocky or sparsely wooded slopes in the Blue Ridge and upper Piedmont from northern North Carolina to central Alabama; also found in the Great Smoky Mountains of Tennessee (FIG. 7).

REPRESENTATIVE COLLECTIONS. **North Carolina.** Burke Co.: trail to "The Chimneys," Table Mountain, *Wilbur 7038* (DUKE, GH, MICH, LL, FSU, GA); Gaston Co.: near top of King's Mountain, *Coker*, 19 May 1919 (FSU, NCU); Lincoln Co.: *Heunter s.n.* (NY); Macon Co.: Highlands, *Harbison*, May 1905 (GH); Madison Co.: *Newberry*, Apr. 1891 (NY); Orange Co.: 4 mi. w. of Hillsborough Exit on Interstate 85, *Weaver 330* (DUKE, GH, US); Polk Co.: Green River Cove, *Weaver 1333* (DUKE, GH, US, NY); Randolph Co.: Carraway Mountain, *Melvin, 22* Apr. 1958 (NCU); Rutherford Co.: Pool Creek, Lake Lure, *Bell 2118* (FSU, NCU); Stokes Co.: Sauratown Mountain, *Radford 34675* (GA, NCU, NY); Surry Co.: slopes of Pilot Mountain, *Oosting 3520* (DUKE, NCU); Transylvania Co.: Thompson River Gorge, *Weaver 360* (DUKE, GH). **South Carolina.** Greenville Co.: Caesar's Head Mountain, *Biltmore Herbarium 708* (GH, US, NY); Oconee Co.: Rich Mountain, *Radford 44707* (NCU). **Georgia.** Bartow Co.: se. of Adairsville, *Duncan & Venard 12339* (GA); Walker Co.: Lula Falls, Lookout Mountain, *Churchill 453* (MO). **Tennessee.** Grainger Co.: Lea Lakes, *Sharp & Underwood 4437* (TENN); Sevier Co.: along Walden Creek, near Cornpone, *Sharp 26818* (DUKE, FSU, GA, GH, NCU, TENN). **Alabama.** Cullman Co.: Cullman, *Mohr*, Apr. 1893 (US); Dekalb Co.: Little River Canyon, *Sherman & Shanks 005* (TENN); Marshall Co.: near Short Creek, *Biltmore Herbarium 708d* (US); St. Clair Co.: 12 mi. w. of Pell City, *McVaugh 8594* (GH).

EXCLUDED NAMES

FOTHERGILLA Aubl. Hist. Pl. Guiane Française **1:** 440. *t. 175.* 1775, *nomen illegit.* Art. 64 = **Miconia** Ruiz & Pav. Prodr. 60. 1794 (Melastomataceae).

FOTHERGILLA INVOLUCRATA Falconer, Proc. Linn. Soc. **1:** 18. 1839, *nomen nudum* = **Parrotiopsis jacquemontiana** (Decne.) Rehder, Jour. Arnold Arb. **1:** 256. 1920 (Hamamelidaceae).

FOTHERGILLA MIRABILIS Aubl. Hist. Pl. Guiane Française **1:** 440. *t. 175.* 1775 = **Miconia mirabilis** (Aubl.) L. O. Williams, Fieldiana Bot. **29:** 574. 1963 (Melastomataceae).

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DEPARTMENT OF BOTANY
DUKE UNIVERSITY
DURHAM, NORTH CAROLINA

THE TRIBE MUTISIEAE (COMPOSITAE) IN THE SOUTHEASTERN UNITED STATES [1]

BERYL SIMPSON VUILLEUMIER

MUTISIEAE Cassini, Jour. Phys. Hist. Nat. Arts **88**: 199. 1819.[2]
(MUTISIA TRIBE)

Subtribe **Gerberinae** Bentham & Hooker, Gen. Pl. **2**: 168, 217. 1873, "Gerberinieae, Gerberae."

A predominantly South American subtribe of about 135 species (sensu Bentham & Hooker) characterized by multiseriate involucres of imbricate bracts, radiate capitula of monochromatic, bilabiate florets (appearing ligulate in ours due to reduction of the inner teeth), long-tailed and terminally appendaged anthers, and rounded style-branch tips.

1. **Chaptalia** Ventenat, Descr. Pl. Jard. Cels. *pl. 61*. 1802.

Perennial rosette herbs with monocephalous, more or less scapose flowering stems. Undersides of basal leaves, scapes, and outer surfaces of the bracts tomentose. Leaves lanceolate or oblanceolate [linear, lyrate, or runcinate], entire, dentate, or lobate [revolute]. Heads turbinate [campanulate], upright [or nodding]; involucres composed of several rows of linear-lanceolate bracts increasing in size toward the inside; receptacles flat, foveolate. Florets trimorphic: the outermost carpellate, lacking stamens, the corolla ligulate with the outer lip tridentate [3] [in

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator Carroll E. Wood, Jr.). The scheme and terminology follow those outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). As in previous treatments, the area includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets. References which the author has not seen are marked by an asterisk.

I am grateful to Dr. Wood for his multifarious help, to Olga Lakela and Robert W. Long, Jr., for living plants of the two species of *Chaptalia* illustrated, and to Donovan Correll and Marshall C. Johnston for some distributional information. The illustration was drawn by Sydney B. Devore (a-e, n) and Irene Brady (f-m).

[2] The tribes of the Compositae have been treated previously by O. T. Solbrig (Jour. Arnold Arb. **44**: 436–461. 1963). The reader should consult this work for additional information (e.g., familial and tribal descriptions, notes, and references) not included here.

[3] Despite Koch's contention that the ray corollas of *Chaptalia* and *Gerbera* which lack an inner lip are distinct from, and not derived from, bilabiate corollas, the pre-

some bilabiate with 1 or 2 minute inner teeth]; the second series of florets also carpellate, lacking stamens, but the corolla reduced to a sheath of variable length (almost absent in *C. dentata*); innermost florets perfect, or functionally staminate due to abortion of the ovule, the corolla bilabiate, or subequal, with the outer lip tripartite and the inner two-parted; corollas uniform in color, white, pale violet, or pink. Style branches of perfect florets thicker and shorter than those of carpellate florets. Pappus setose-capillary, copious, white or pinkish. Achenes fusiform, 5- to several-nerved, glabrous or sparsely villous [papillose], usually beaked (beakless in *C. tomentosa*), topped by the pappus. TYPE SPECIES: *C. tomentosa* Vent. (Named for Count Chaptal de Canteloupe, 1756–1832, a French chemist who published several works on economically important plants, including a study of the resins of *Pinus* species and methods of improving the wine grape.) — SUNBONNETS.

A genus of about 53 species grouped into seven sections (Burkart). Six species [4] representing four of the sections occur in the United States, but the majority of the species is found in the Greater Antilles, Central America, and South America (south to northern Chile and Argentina).

Although three genera of the Mutisieae occur in the United States (*Chaptalia* and two members of the subtribe Nassauviinae: *Perezia*, with 5 species, and *Trixis*, with two species), only two species occur in the Southeast. *Chaptalia tomentosa*, pineland daisy, of sect. CHAPTALIA, is endemic to the pinelands of the Coastal Plain from southeastern North Carolina to southern Florida, west to eastern Texas. *Chaptalia dentata* (L.) Cass., of sect. LIEBERKUHNA (Cass.) Burkart, is primarily West Indian in distribution,[5] but has several scattered populations in the pinelands of subtropical Florida. These two species are placed in different sections because the central florets of *C. tomentosa* are functionally staminate, while those of *C. dentata* are perfect; but the two species are more easily separated by their achenes (long beaked in *C. dentata* and beakless in *C. tomentosa*), by the length of the ligulate corollas, and by the position of the heads before and after anthesis (see illustration).

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dominance of bilabiate "ray" florets in *Gerbera*, the vestiges of an inner lip in many species of *Chaptalia*, and the tridentate ligule in corollas lacking an inner lip, all indicate that in these two genera, the ligulate ray florets are derived from bilabiate forms by loss of the inner lip.

[4] Burkart recorded only *Chaptalia alsophila* Greene, *C. dentata* (L.) Cass., *C. tomentosa*, and *C. nutans* (L.) Polak. as occurring in the United States, but Watson (Proc. Am. Acad. Arts Sci. **23**: 265. 1888) recorded *C. Seemannii* (Sch. Bip.) Hemsl. from Mexico and Arizona, and Kearney & Peebles (Ariz. Fl. ed. 2. 957. 1960) listed *C. leucocephala* Greene as occurring from Arizona to Mexico and added New Mexico to the range of *C. Seemannii*.

[5] Standley (Fieldiana Bot. 3(3): 441. 1930) mentioned that *Chaptalia dentata* was cultivated at two localities in Yucatán. Burkart, however, referring to the original reference (Millspaugh & Chase, Fieldiana Bot. 3(2): 148. 1904) decided that the species involved was actually the closely related *C. obovata* Wright. Burkart did cite, however, one specimen of *C. dentata* from Huasteca, Veracruz, Mexico.